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# A reassessment of large theropod dinosaur tracks from the mid-Cretaceous (late Albian–Cenomanian) Winton Formation of Lark Quarry, central-western Queensland, Australia: A case for mistaken identity

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## ABSTRACT

Multivariate analysis is used to differentiate shape variations between ichnites of theropod and ornithopod dinosaurs. Tracks of an alleged theropod cf. *Tyrannosauropus* from the mid-Cretaceous (late Albian–Cenomanian) Winton Formation of Lark Quarry, central-western Queensland, Australia were examined and foot shape ratios calculated. Multivariate analysis of these shape variables indicates this track-maker was an ornithopod dinosaur. A strong morphological similarity exists between the Lark Quarry ichnites and those of the iguanodontian ichnotaxon *Amblydactylus gethingi*. Considering the grade of ornithopod this ichnogenus is thought to represent (a non-hadrosaurid styracosternan) and the age and geography of Lark Quarry, we suggest that the track-maker may have been a dinosaur similar to *Muttaborrasaurus langdoni*.

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## 1. Introduction

A primary goal within the study of ichnology is to determine the identity of the trace-maker. Trace fossils in the form of tracks produced by tetrapods can provide a wealth of information on foot morphology (Thulborn, 1990; Irby, 1995; Lockley et al., 2006b), body posture (Gierlinski, 1994; Moratalla et al., 1994; Wilson and Carrano, 1999; Milner et al., 2009), locomotor ability (Alexander, 1976; Thulborn and Wade, 1989; Moratalla et al., 1994; Gatesy et al., 1999; Mazzetta and Blanco, 2001; Day et al., 2002; Dalman, 2006; Ezqerra et al., 2007), sociality (Lockley and Matsukawa, 1999; Barco et al., 2006; Lockley et al., 2006a), preferential environments (Lockley, 1991) as well as stratigraphic and geographic faunal diversity (Melchor et al., 2002; Matsukawa et al., 2005; Moreno and Benton, 2005; Paik et al., 2006; Mateus and Milan, 2008). The morphology of dinosaur footprints usually reflect the often unique characteristics of the track-maker's foot skeleton (toe number and symmetry, footprint length to width ratios; Lockley, 1991; Carrano and Wilson, 2001), and so identifying the prints made by dinosaurs such as sauropods, stegosaurs and ceratopsians can be done relatively easily. Challenges may arise in distinguishing tracks of bipedal theropod and ornithopod dinosaurs. These can

appear quite similar with both possessing feet that are functionally tridactyl with mesaxonic toe symmetry (Thulborn, 1994; Fastovsky and Smith, 2004; Lockley, 2009). General criteria exist to help differentiate 'typical' ornithopod and theropod dinosaur tracks (Mateus and Milan, 2008), but within each clade occur wide range of morphological variation, and the morphological similarity between clades can make identification difficult.

The Dinosaur Stampede National Monument (Australian Natural Heritage List, Place ID 105664) at Lark Quarry Conservation Park, 95 km south-west of Winton, central-western Queensland, Australia, captures the movements of dozens of dinosaurs and contains thousands of individual footprints (Thulborn and Wade, 1979, 1984). The tracks, which are preserved in silt- to very fine sandstone of the mid-Cretaceous (late Albian–Cenomanian, Winton Formation), have been interpreted as preserving the apparent pursuit of a mixed herd of small-bodied dinosaurs by an *Allosaurus*-sized theropod dinosaur. These accounts have led to the popular concept of the moment of a dinosaur 'stampede' captured in time (Molnar, 1991; Rich and Vickers-Rich, 2003). In their account of the Lark Quarry trackways, Thulborn and Wade (1984) recognised three ichnotaxa: *Wintonopus latomorum* (attributed to a small-bodied ornithopod), *Skartopus australis* (attributed to a small-bodied theropod) and cf. *Tyrannosauropus* (attributed to a likely large-bodied theropod).

A central aspect to the Lark Quarry dinosaur stampede scenario is the identification of the large tridactyl trackway (Fig. 1) as the

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predatory protagonist. Thulborn and Wade (1984) originally referred these tracks to cf. *Tyrannosauropus* sensu Haubold (1971), considering them to be “closer in appearance to *Tyrannosauropus* than to any other form of carnosaur footprint so far described” (Thulborn and Wade, 1984, p 420). As with many tridactyl dinosaur ichnotaxa, *Tyrannosauropus* has a checkered history. Lessertisseur (1955, p. 116) proposed that the name *Tyrannosauripus* (spelt with an ‘i’) could be used for tracks purportedly made by *Tyrannosaurus rex* and illustrated by Peterson (1924), themselves based on multiple poorly described specimens from several localities and horizons in coal mines in the Campanian Mesa Verde Formation, Utah (Carpenter, 1992). Lessertisseur (1955) did not assign the name to any particular ichnite from Peterson’s (1924) publication, and the ichnotaxon has consequently been placed in *nomen dubium* (Lockley and Hunt, 1994). With this name now available, *Tyrannosauripus* was adopted by Lockley and Hunt (1994) who assigned it to a large track specimen from the Upper Cretaceous Raton Formation, New Mexico.

*Tyrannosauropus petersoni* (spelt with an ‘o’) was erected by Haubold (1971) for unspecified tracks illustrated in Peterson (1924). The majority of these tracks are now considered to be attributable to a hadrosaurid ornithopod (Brown, 1938; Carpenter, 1992; Lockley and Hunt, 1994; Manning, 2008). Given that the Lark Quarry tracks were compared to this ichnogenus by Thulborn and Wade (1979, 1984), it therefore follows that they may also have been made by an ornithopod. On at least three occasions since their discovery it has been suggested that the Lark Quarry cf. *Tyrannosauropus* tracks were made by an ornithopod (Norman p. 421 cited in Thulborn and Wade, 1984; Paul, 1988; Lockley and Hunt, 1994), but none of these claims has been substantiated by detailed analysis. The confusion surrounding *Tyrannosauropus* tracks, both at Lark Quarry and elsewhere highlights the difficulties associated

Fig. 1. *Amblydactylus* cf. *A. gethingi*, Winton Formation, Lark Quarry, central-western Queensland; tracks 3–7 (cast). Photograph © Queensland Museum, Bruce Cowell.

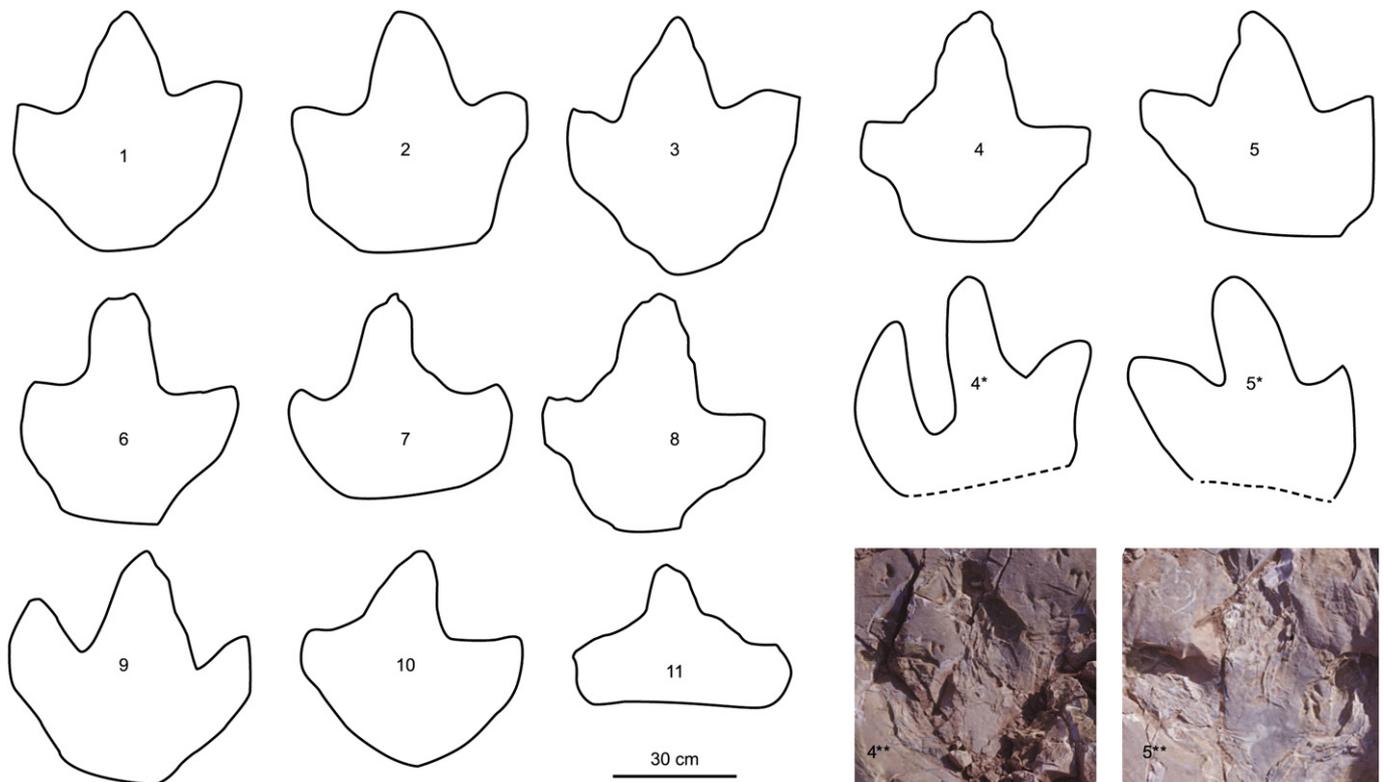


Fig. 2. *Amblydactylus* cf. *A. gethingi*, Winton Formation, Lark Quarry, central-western Queensland; outlines of tracks 1–11 from Thulborn and Wade (1984); tracks 4\* and 5\* from Thulborn and Wade (1979). Photographs of tracks 4\*\* and 5\*\* © Queensland Museum.

**Table 1**

Parameters used to discriminate between theropod and ornithopod tracks. Track parameters, threshold values and percentage theropod/ornithopod probability. Adapted from Moratalla et al. (1988) and Mateus and Milan (2008). See Fig. 3B and Materials and methods for explanations of track parameters.

Track Parameters	Threshold values and probability that the track is either theropod or ornithopod	Average for tracks 1–11 (Thulborn and Wade, 1984)
L/W	80.0% Theropod > 1.25 > Ornithopod 88.2%	0.99
L/K	70.5% Theropod > 2.00 > Ornithopod 88.0%	1.58
L/M	65.0% Theropod > 2.00 > Ornithopod 90.7%	1.64
BL2/WM2	76.1% Theropod > 2.00 > Ornithopod 97.7%	0.87
BL4/WM4	76.1% Theropod > 2.00 > Ornithopod 97.7%	0.92
BL3/WM3	72.7% Theropod > 2.20 > Ornithopod 97.7%	1.67
L2/WB2	84.6% Theropod > 3.75 > Ornithopod 90.2%	2.77
L4/WB4	73.7% Theropod > 3.75 > Ornithopod 93.4%	2.70
L3/WB3	70.6% Theropod > 4.00 > Ornithopod 91.5%	2.11

with discerning the track-maker identity of tridactyl dinosaur prints.

Here we apply the multivariate analysis used by Moratalla et al. (1988) and Mateus and Milan (2008) to discriminate between theropod and ornithopod tracks to reassess the identity of the Lark Quarry 'carnosaur'. This work presents the first multivariate analysis applied to any of the Lark Quarry dinosaur tracks.

## 2. Material and methods

Measurements were made on the cf. *Tyrannosauropus* tracks using published line drawings (Thulborn and Wade, 1979, 1984), catalogued photographs, latex peels, and various casts held in the Queensland Museum (QM), Brisbane, Australia (Figs. 1 and 2), along with firsthand examination of the tracks themselves. Following Moratalla et al. (1988), tracks were analysed using the following parameters (Fig. 3 and Table 1): track length (L), track width (W), total digit lengths (L2–4), basal digit lengths (BL2–4), basal digit widths (WB2–4), middle digit widths (WM2–4) and the distance from 'heel' to the interdigital (hypex) point (K, M). These parameters were applied to each of the eleven tracks figured by Thulborn and Wade (1984), along with additional measurements for tracks

4 and 5 as figured by Thulborn and Wade (1979), and photographs and casts of these same two tracks in the collections of the Queensland Museum.

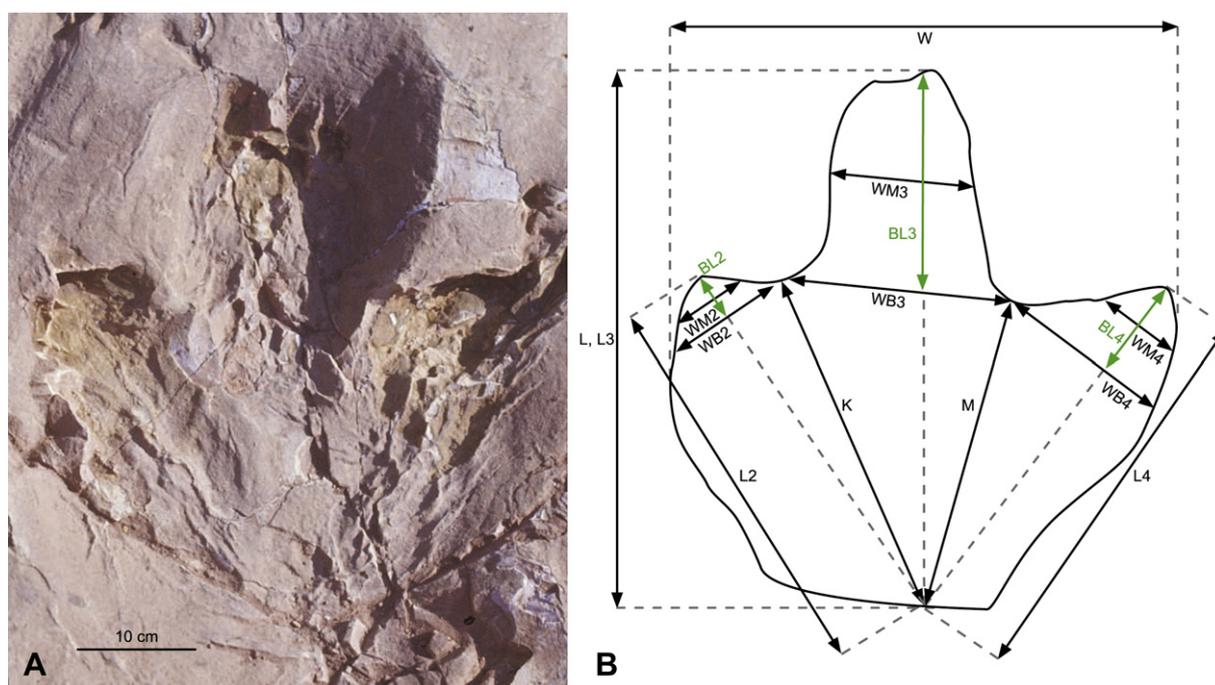
We considered it prudent to collect new data from the Lark Quarry tracksite and cast material. The latter is considered more informative since the former has undergone considerable alteration since excavation (Agnew et al., 1989). Upon our direct examination of the tracks and casts as well as the photographs of the tracks, we are in agreement with the track outlines provided by Thulborn and Wade (1984).

Rather than solely using tables of numbers to illustrate each data point's proximity to track-maker threshold values (Mateus and Milan, 2008), bi-coloured columns were constructed for each track parameter and colour separated at their respective threshold value.

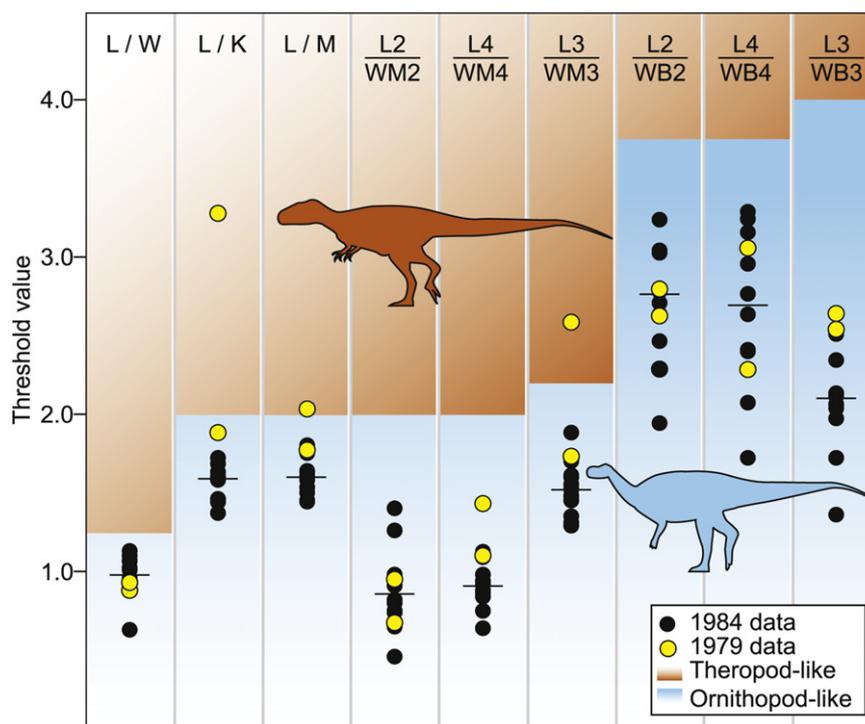
## 3. Results and discussions

### 3.1. Ichnotaxonomy

The majority of results of the multivariate analysis (Fig. 4 and Appendix 1) fall within the threshold expected for ornithopod dinosaurs (Moratalla et al., 1988). In fact, all the measurements



**Fig. 3.** *Amblydactylus* cf. *A. gethingi*, Winton Formation, Lark Quarry, central-western Queensland; track 6; A, photograph. B, outline with analysis markers. L: track length. W: track width. L2–4: whole digit length. BL2–4: basal digit lengths. WB2–4: basal digit widths. WM2–4: middle digit widths. K, M: "heel" to interdigital (hypex) lengths. Adapted from Moratalla et al. (1988). Photograph © Queensland Museum.



**Fig. 4.** Multivariate analysis of the foot measurements of the Lark Quarry ‘carnosaur’. Black circles: tracks 1–11 from illustrations from Thulborn and Wade (1984). Yellow circles: tracks 4 and 5 from illustrations from Thulborn and Wade (1979). L: track length. W: track width. L2–4: whole digit length. BL2–4: basal digit lengths. WM2–4: middle digit widths. K, M: “heel” to interdigital (hypex) lengths. Horizontal lines are average values of tracks 1–11.

taken from Thulborn and Wade (1984) produced values expected for an ornithopod track-maker. Measurements taken from Thulborn and Wade (1979) for tracks 4 and 5 produced a majority of data points expected for an ornithopod track-maker. Only two values for track 4 and one value for track 5 would indicate theropod affinities based on data derived from the 1979 publication. These three data points are for the relationships between L/K, L/M (the total length to ‘heel’ to hypex length of digit two and four, respectively) and BL3/WB3 (the total length of the middle digit to the basal width of the middle digit). When measured again using catalogued photographs and casts, track 5 had values that correspond with those of an ornithopod track-maker, and damage to track 4 enabled only four threshold values to be calculated. Of these, three values revealed an ornithopod affinity (L/W, BL2/WM2 and L2/WB2) and one value revealed a theropod affinity (BL3/WB3).

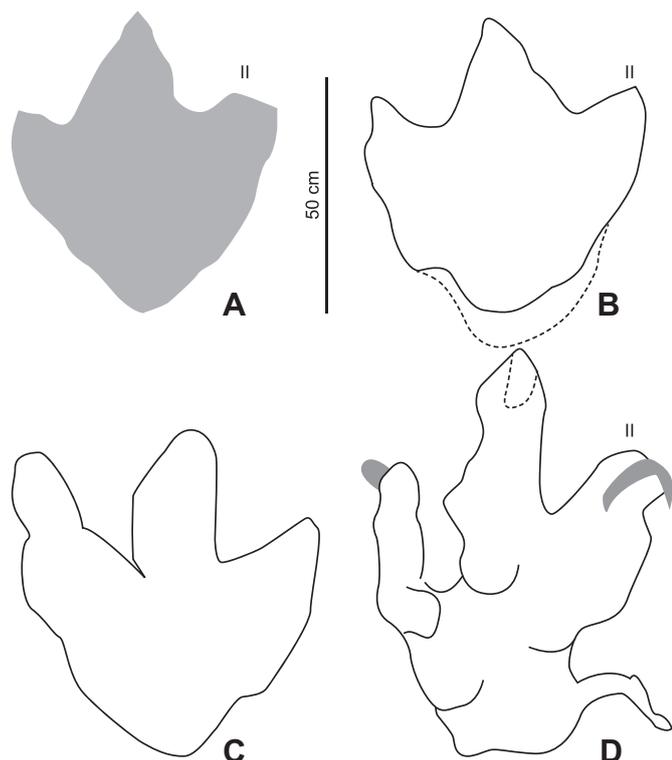
The multivariate analysis strongly supports ornithopod affiliation for the large tridactyl tracks at Lark Quarry. However, several threshold values obtained for tracks 4 and 5 (Appendix 1; Thulborn and Wade, 1979, 1984) also support a theropod affiliation, highlighting the fact that the precise outline of these tracks is difficult to ascertain and potentially contentious. Even when the outlines given by Thulborn and Wade (1979) are used, there is still only weak support (3 out of 18 characteristics) that tracks 4 and 5 pertain to a theropod track-maker. When measurements were taken from photographs of these tracks and direct examination of casts, the data points for theropod affinities disappeared, whilst track 4 was considered too damaged for a full data set, one value fell in the range of theropods and three values for ornithopods. Based on the overall data, we therefore reject the theropodan affinities of this track-maker (Fig. 4).

At least two different types of theropods are known from the Winton Formation based on body fossils. Salisbury (2003) reported on the occurrence of shed teeth referable to a small dromaeosaurid-like theropod, while Hocknull et al. (2009) described the medium-

sized theropod *Australovenator wintonensis* based on a partial associated skeleton. Hocknull and Cook (2010) regarded it “probable that the large theropod track-maker at the Lark Quarry Dinosaur stampede was a lone individual [of] *Australovenator*, stalking smaller ornithopod prey by the lake shore.” However, *Australovenator* is a medium-sized theropod with an estimated height at the hips of 1.6 m (Hocknull et al., 2009, fig. 2d) and is a poor match as the large Lark Quarry track-maker with a calculated hip height of between 2.54 and 2.68 m (Thulborn and Wade, 1984, p. 436). Hocknull et al. (2009) originally described *Australovenator* as a basal allosauroid, but more recently it has been reconsidered as a megaraptoran carcharodontosaurian (Benson et al., 2010; Agnolin et al., 2010), confirming the presence of *Megaraptor*-like theropods in Australia proposed by Salisbury et al. (2007) and Smith et al. (2008). In considering *Australovenator* or a closely related taxon as a possible candidate for the Lark Quarry track-maker, the Comanchean theropod tracks *Irenesauripus* (Pittman, 1989), potentially made by the carcharodontosaurian *Acrocanthosaurus* (Langston, 1974; Farlow, 2001), were scaled to the size of the reconstructed foot of *Australovenator* (Fig. 6). The outline and size of the inferred *Australovenator* footprint does not correspond to any of the ‘carnosaur’ tracks made at Lark Quarry. As such *Australovenator* is not considered as a track-maker at the site. Instead, the inferred *Australovenator* footprint shows much stronger similarities with the Australian theropod ichnospecies *Megalosauropus broomensis* (Fig. 6).

None of the tracks from Thulborn and Wade (1984) produced multivariate data supporting the idea that the track-maker was a theropod, nor does the footprint morphology of the Lark Quarry tracks resemble those attributed to theropods. From these results, we agree with Norman (p. 421 cited in Thulborn and Wade, 1984), Paul (1988) and Lockley and Hunt (1994) that the maker of the large tridactyl tracks at Lark Quarry was an ornithopod.

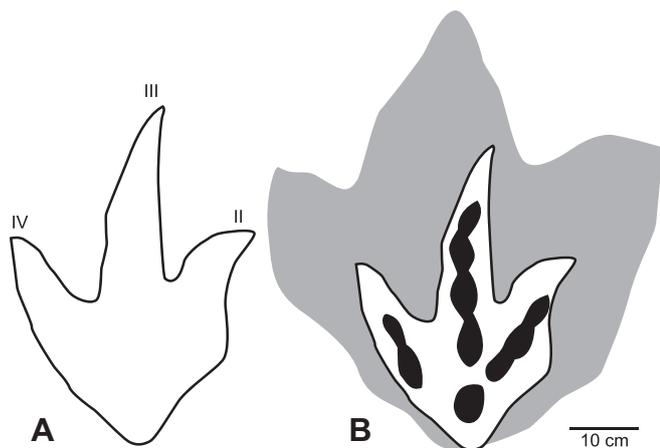
So what sort of ornithopod dinosaur made the large tridactyl prints at Lark Quarry? Thulborn and Wade (1984) based their



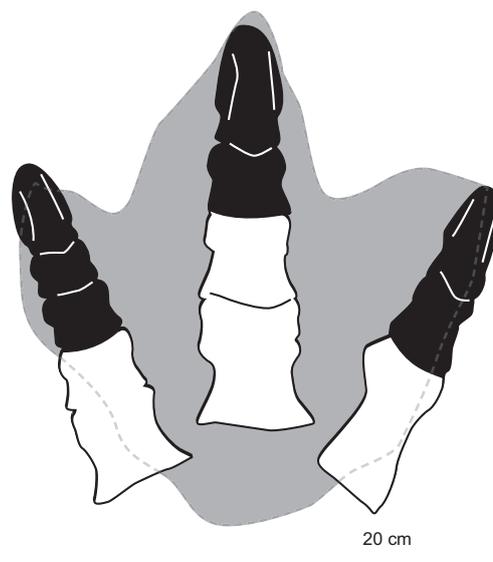
**Fig. 5.** Comparison of tridactyl dinosaur footprints. A, *Amblydactylus* cf. *A. gethingi* (Lark Quarry, track 3; ornithopod); B, *Amblydactylus gethingi* (ornithopod; reversed); C, “*Tyrannosauropus petersoni*” (ornithopod); D, *Tyrannosauripus pillmorei* (theropod; reversed). Adapted from Thulborn and Wade (1984), Currie and Sarjeant (1979), Haubold (1971), Lockley and Hunt (1994).

theropod argument on four distinct features that we use here to determine a likely ornithopod ichnogenus. These distinctive features are:

1. The footprints are slightly longer than wide;
2. The toes are symmetrical;
3. The presence of claws;
4. The presence of a V-shaped central digit.



**Fig. 6.** Comparison of the Lark Quarry *Amblydactylus* cf. *A. gethingi* tracks with those of selected theropods. A, theropod track *Irenesauripus* (a likely carcharodontosaurian). B, theropod track *Irenesauripus* scaled to the expected maximum size of a reconstructed *Australovenator wintonensis* footprint (white), with the track of *Megalosauropus broomensis* (black; reversed) superimposed onto track 3 from Lark Quarry (see text for details). Adapted from Lockley et al. (1998), Pittman (1989), Thulborn and Wade (1984).

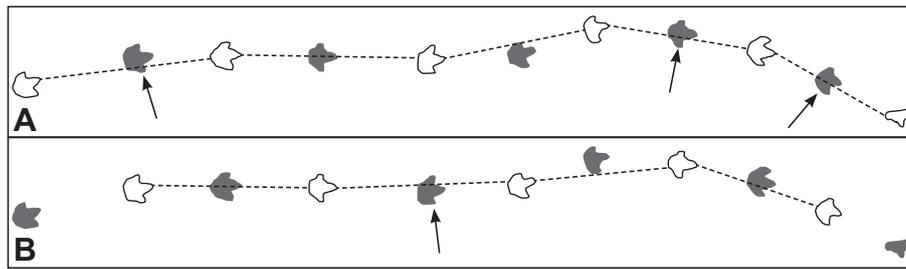


**Fig. 7.** Comparison of track 3 of *Amblydactylus* cf. *A. gethingi* from Lark Quarry with the reconstructed right pes (reversed) of *Muttaborrasaurus langdoni*. Preserved elements are shown in white following Molnar (1996); black portions have been reconstructed based on the pes morphology of closely related large iguanodontians. The outline of the Lark Quarry track is adapted from Thulborn and Wade (1984).

Of the large Cretaceous ornithopod ichnogenera, Lockley and Wright (2001) considered only *Amblydactylus*, *Caririchnium* and *Iguanodontipus* as valid. Of these, only the iguanodontian ichnogenus *Amblydactylus* (Sternberg, 1932) shares distinctive characteristics with the Lark Quarry tracks (Fig. 5). When *Amblydactylus* is compared with the best-preserved Lark Quarry ichnite (track 3 following Thulborn and Wade, p. 434, 1984), they share distinct features including footprint length greater than width; good toe symmetry; pointed ‘hooves’; digits being proximally broad, but tapering distally. In addition, both ichnites also have a similarly prominent ‘heel’. Sternberg (1932, p. 72) defined *Amblydactylus* based on tracks from the Early Cretaceous (Barremian–early Albian) Gething Formation of the Bullhead Group of western Canada. Currie and Sarjeant (1979, p. 105) emended Sternberg’s diagnosis of *Amblydactylus* as follows:

“Bipedal, with three functional pedal digits. The outer contours of digits II and IV diverge at low angles from the longitudinal axis of the ichnite. A metatarsal-phalangeal pad produces a distinct posterior impression. Interdigital webs link the proximal portions of the fleshy digital pads; the digits end in blunt claws or pointed hooves. The ichnite is almost as wide as, or wider than, it is long.”

Some examples of *Amblydactylus* include manus impressions (Currie, 1983; Lockley and Wright, 2001) indicating that the track-maker was a facultative quadruped, but this feature is not diagnostic for the ichnogenus. Of the illustrated tracks (Fig. 5), the resemblance between the Lark Quarry ichnite and the type specimen of ichnospecies *Amblydactylus gethingi* is striking. Sternberg (1932) noted the tracks of *Amblydactylus gethingi* were too large to be made by *Camptosaurus*. Likely camptosaur tracks have since been identified (*Dinehichnus*; Gierlinski and Sabath, 2008) and are recognised by their smaller size and more gracile morphology when compared with tracks of *Amblydactylus gethingi*. Sternberg (1932) described the tracks of *Amblydactylus gethingi* as possessing hoof impressions that were too pointed to have been made by a hadrosaurid, but noted that they did show some resemblance to tracks made by *Iguanodon*. No bones of ‘iguanodontids’ or hadrosaurids had been found in the Gething Formation to allow Currie and Sarjeant (1979) to determine a likely *Amblydactylus gethingi* track-maker, although they noted that the footprint outlines more



**Fig. 8.** *Amblydactylus* cf. *A. gethingi*, Winton Formation, Lark Quarry, central-western Queensland. A, Left-footprint strides (dotted line) with the right footprint crossing the midline (grey). B, Right-footprint strides (dotted line) with the left footprint crossing the midline (grey). Outline of Lark Quarry trackway adapted from Thulborn and Wade (1984).

closely resembled those of hadrosaurids than ‘iguanodontids’ (p. 112). Currie (1983) found that the majority of tracks attributable to this ichnospecies appear to have blunt hooves providing support for a hadrosaurid track-maker but also noted that the type specimen had hooves sharper than expected for a hadrosaurid and that the date of the tracks were significantly older than body fossils for the clade. Thulborn (1990, p. 198) considered this assignment to a hadrosaurid track-maker questionable, and Lockley (1991, p. 56) described the tracks of *Amblydactylus* as most likely having been made by an *Iguanodon*-like species.

Since some, but not all of the Lark Quarry tracks display pointed hoof/ungual impressions, we are of the opinion that this represents an anatomical feature of the foot of this track-maker, and that it is therefore likely the track-maker was a large iguanodontian ornithopod, but not a hadrosaurid. We therefore propose that the large tridactyl tracks from Lark Quarry should be referred to *Amblydactylus* cf. *A. gethingi*.

### 3.2. Possible track-maker

If our interpretation of the large tridactyle tracks at Lark Quarry is correct, it is possible to speculate on a likely track-maker in light of known Australian ornithopod body fossils. Such a candidate must be of similar stratigraphic age, provenance, phylogenetic affinity, body mass dimension and comparable foot size and shape (Farlow, 2001) as the Lark Quarry ichnofossils. Following Agnolin et al. (2010), valid Australian Cretaceous ornithopod taxa include: *Muttaborrasaurus langdoni* and *Muttaborrasaurus* sp., both from the late Albian–early Cenomanian of central-western Queensland (Bartholomai and Molnar, 1981; Molnar, 1996); *Leallynasaura amigraphica* from the late Aptian–early Albian of Dinosaur Cove, southern Victoria (Rich and Rich, 1989); and *Qantasaurus intrepidus*, from the early Aptian of Flat Rocks, southern Victoria (Rich and Vickers-Rich, 1999). A number of unnamed specimens from other Early–mid-Cretaceous sites in Queensland, northwestern NSW and southern Victoria, can also be identified as pertaining to non-dryomorph ornithopods (Agnolin et al., 2010; pers. obs. SWS). Of these taxa, the styracosternan iguanodontian *Muttaborrasaurus* represents the best match for the *Amblydactylus* track-maker at Lark Quarry.

The type specimen of *Muttaborrasaurus langdoni* (QM F6140) comes from the upper part of the Mackunda Formation (late Albian–early Cenomanian; Gray et al., 2002), near Rock Hole, Thomson River, ‘Rosebery Downs’ Station, southwest of Muttaborra, central-western Queensland, Australia (Bartholomai and Molnar, 1981). Specimens referred to *Muttaborrasaurus* sp. (QM F14921 and QM F12541) come from the Allaru Mudstone (late Albian–early Cenomanian; Gray et al., 2002), at localities on Dunluce Station (between Hughenden and Richmond) and Iona Station (southeast of Hughenden), respectively, both in central-western, Queensland, Australia (Molnar, 1996). All these occurrences are not too distant from Lark Quarry Conservation Park and are in units that

are either slightly older or equivalent in age to the Winton Formation in which the Lark Quarry ichnites occur. Agnolin et al. (2010) regarded both species of *Muttaborrasaurus* as non-hadrosaurid styracosternan ornithopods, an assignment that would be consistent with the inferred track-maker for the *Amblydactylus* ichnites (Sternberg, 1932).

The body size of the Lark Quarry track-maker has been calculated as between 2.54 and 2.68 m at the hip (Thulborn and Wade, 1984, p. 436). This is a good match for the hip height of *Muttaborrasaurus langdoni*, estimated to be between 2.5 m (Molnar, 1996, fig. 9) and 3 m (Bartholomai and Molnar, 1981). Norman (2004) noted that similar grade large ornithopods with functionally tridactyl pes have blunt ended unguals that are dorsoventrally flattened. In life, the blunt unguals may have been covered in a pointed horny sheath as revealed in tracks attributed to *Iguanodon* (Moratalla et al., 1994; Lockley and Meyer, 2000). The foot skeleton of *M. langdoni* is also comparable in size and shape to Lark Quarry track 3 (Fig. 7), although there is some discrepancy with the details of the reconstruction of the pes of *M. langdoni* and subsequent print outline since the distal digits and unguals are not known and do not account for the pointed hooves likely for this species. We consider here that *Muttaborrasaurus*, or a closely related taxon, is the most likely candidate for the maker of the large Lark Quarry footprints.

Thulborn and Wade (1984) describe the Lark Quarry track-maker as having a walking progression with a “definite tendency to decelerate” along a “slightly weaving course” (p. 436). However, this interpretation may be incorrect. At several points along the trackway the left foot crosses over the right and the right crosses over the left (tracks two, five, eight and ten; Fig. 8). Breithaupt et al. (2006) suggest that when this occurs in bipedal dinosaur trackways, the animal may not be in continuous motion, and potentially stopping in midstride. This would also suggest that the walking speeds previously calculated for this track-maker by Thulborn and Wade (1984) may be misleading.

If our conclusion is valid, then the original Lark Quarry site interpretation as a prey-pursuit scenario is incorrect. Whilst we currently accept the interpretation by Thulborn and Wade (1979, 1984) that many dozens of smaller dinosaurs were running at the site, we consider it unlikely that the ‘stampede’ was caused by the presence of the large ornithopod. Finally, if the large Lark Quarry track-maker was an ornithopod then it removes any published evidence for the presence of large (i.e., *Allosaurus*-sized or larger) theropod dinosaurs in the Australian Cretaceous.

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## References

- Agnew, N., Griffin, H., Wade, M., Tebble, T., Oxnam, W., 1989. Strategies and techniques for the preservation of fossil tracksites: an Australian example. In: Gillette, D.D., Lockley, M.G. (Eds.), *Dinosaur Tracks and Traces*. Cambridge University Press, pp. 397–407.
- Agnolin, F.L., Ezcurra, M.D., Pais, D.F., Salisbury, S.W., 2010. A reappraisal of the Cretaceous non-avian dinosaur faunas from Australia and New Zealand: evidence for their Gondwanan affinities. *Journal of Systematic Palaeontology* 8, 257–300.
- Alexander, R.M.C.N., 1976. Estimates of speeds of dinosaurs. *Nature* 261, 129–130.
- Barco, J.L., Canudo, J.I., Ruiz-Omenaca, J.I., 2006. Gregarious behaviour in theropods. *Ichnos* 13, 237–248.
- Bartholomai, A., Molnar, R.E., 1981. *Muttaborrasaurus*, a new iguanodontid (ornithischia: ornithopoda) dinosaur from the Lower Cretaceous of Queensland. *Memoirs of the Queensland Museum* 20, 319–349.
- Benson, R.B.J., Carrano, M.T., Brusse, S.L., 2010. A new clade of archaic large bodied predatory dinosaurs (Theropoda: Allosauroidea) that survived to the latest Mesozoic. *Naturwissenschaften* 97, 71–78.
- Breithaupt, B., Southwell, E.H., Matthews, N.A., 2006. Abstracts with Programs. *Walking with Emus: Insights into Dinosaur Tracking in the 21st Century*, vol. 38. Geological Society of America, p. 537.
- Brown, B., 1938. The mystery dinosaur. *Natural History* 41, 190–202, 235.
- Carpenter, K., 1992. Contributions to Geology, University of Wyoming. Behavior of Hadrosaurs as Interpreted from Footprints in the “Mesaverde” Group (Carnian) of Colorado, Utah, and Wyoming, vol. 29, pp. 81–96.
- Carrano, M.T., Wilson, J.A., 2001. Taxon distributions and the tetrapod track record. *Paleobiology* 27, 564–582.
- Currie, P.J., 1983. Hadrosaur trackways from the Lower Cretaceous of Canada. *Acta Paleontologica Polonica* 28, 63–73.
- Currie, P., Sarjeant, W.A.S., 1979. Lower Cretaceous dinosaur footprints from the Peace River Canyon, British Columbia, Canada. *Palaeogeography Palaeoclimatology Palaeoecology* 28, 103–115.
- Dalman, S., 2006. Footprint morphology and biomechanics of small ornithischian dinosaur ichnogenus *Anomoepus* from the lower Jurassic of Western Massachusetts. *Journal of Vertebrate Paleontology* 26, 54A.
- Day, J.J., Norman, D.B., Upchurch, P., Powell, H.P., 2002. Dinosaur locomotion from new trackway. *Nature* 415, 494–495.
- Ezquerro, R., Doublet, S., Costeur, L., Galton, P.M., Pérez-Lorente, F., 2007. Were non-avian theropod dinosaurs able to swim? Supportive evidence from an early Cretaceous trackway, Cameros Basin (La Rioja, Spain). *Geology* 35, 507–510.
- Farlow, J.O., 2001. *Acrocanthosaurus* and the maker of the Comanche large theropod footprints. In: Carpenter, K., Tanke, D. (Eds.), *Mesozoic Vertebrate Life*. New research inspired by the palaeontology of Philip J. Currie. Indiana University Press, pp. 408–427.
- Fastovsky, D.E., Smith, J.B., 2004. Dinosaur paleoecology. In: Weishampel, D.B., Dodson, P., Osmólska, H. (Eds.), *The Dinosauria*. University of California Press, Berkeley and Los Angeles, pp. 614–626.
- Gatesy, S.M., Middleton, K.M., Jenkins, F.A., Shubin, N.H., 1999. Three dimensional preservation of foot movements in Triassic theropod dinosaurs. *Nature* 399, 141–144.
- Gierlinski, G., 1994. Early Jurassic theropod tracks with metatarsal impressions. *Przeglad Geologiczny* 42, 280–284.
- Gierlinski, G.D., Sabath, K., 2008. Stegosaurian footprints from the Morrison formation of Utah and their implications for interpreting other ornithischian tracks. *Oryctos* 8, 29–46.
- Gray, A.R.G., McKillop, M., McKellar, J.L., 2002. Eromanga basin stratigraphy. In: Draper, J.J. (Ed.), *Geology of the Cooper and Eromanga Basins, Queensland*. Department of Natural Resources and Mines, Brisbane, pp. 30–56.
- Haubold, H., 1971. *Ichnia Amphibiorum et Reptiliorum Fossilium*. In: Kuhn, O. (Ed.), *Handbuch der Paläoherpetologie*, vol. 18. Gustav Fischer, pp. 1–123.
- Hocknull, S., Cook, A., 2010. Dragons, diprotodons, dinosaurs and dust: 150 million years of desert channels prehistory. In: Robin, L., Dickman, C., Martin, M. (Eds.), *Desert Channels. The Impulse to Conserve*. CSIRO Publishing, pp. 210–223.
- Hocknull, S.A., White, M.A., Tischler, T.R., Cook, A.G., Calleja, N.D., Sloan, T., Elliott, D.A., 2009. New Mid-Cretaceous (Latest Albian) dinosaurs from Winton, Queensland, Australia. *PLoS ONE* 4, e6190.
- Irby, G.V., 1995. Posterolateral markings on dinosaur tracks, Cameron dinosaur tracksite, Lower Jurassic Moenave Formation, northeastern Arizona. *Journal of Paleontology* 69, 779–784.
- Langston, W., 1974. Non-mammalian Comanchean tetrapods. *Geoscience and Man* 8, 77–102.
- Lessertisseur, I., 1955. Traces fossiles d'activité animale et leur signification paléobiologique. *Memoires de la Société géologique de France* 74, 1–149.
- Lockley, M., Meyer, C., 2000. *Dinosaur Tracks and Other Fossil Footprints of Europe*. Columbia University Press, p. 323.
- Lockley, M.G., 1991. *Tracking Dinosaurs: A New Look at an Ancient World*. Cambridge University Press, Cambridge, p. 238.
- Lockley, M.G., 2009. New perspectives on morphological variation in tridactyl foot prints: clues to widespread convergence in developmental dynamics. *Geological Quarterly* 53, 415–432.
- Lockley, M.G., Hunt, A.P., 1994. A track of the giant theropod dinosaur *Tyrannosaurus* from close to the Cretaceous/Tertiary Boundary, northern New Mexico. *Ichnos* 3, 213–218.
- Lockley, M.G., Houck, K., Yang, S.Y., Matsukawa, M., Lim, S.K., 2006a. Dinosaur-dominated footprint assemblages from the Cretaceous Jindong Formation, Hallyo Haesang national park area, Goseong County, South Korea: evidence and implications. *Cretaceous Research* 27, 70–101.
- Lockley, M.G., Matsukawa, M., 1999. Some observations on trackway evidence for gregarious behavior among small bipedal dinosaurs. *Palaeogeography Palaeoclimatology Palaeoecology* 150, 25–31.
- Lockley, M.G., Matsukawa, M., Sato, Y., Polahan, M., Daorerk, V., 2006b. A distinctive new theropod dinosaur track from the Cretaceous of Thailand: implications for theropod track diversity. *Cretaceous Research* 27, 139–145.
- Lockley, M.G., Meyer, C.A., Santos, V.F., 1998. *Megalosauiripus* and the problematic concept of megalosauiripus footprints. *Gaia* 15, 313–337.
- Lockley, M.G., Wright, J.L., 2001. Trackways of large quadrupedal ornithopods from the Cretaceous: a review. In: Carpenter, K., Tanke, D. (Eds.), *Mesozoic Vertebrate Life*. New research inspired by the palaeontology of Philip J. Currie. Indiana University Press, pp. 428–442.
- Manning, P.L., 2008. *T. rex* speed trap. In: Carpenter, K., Larson, P.L. (Eds.), *Tyrannosaurus rex; the tyrant king*. Indiana University Press, pp. 204–231.
- Mateus, O., Milan, J., 2008. Ichological evidence for giant ornithopod dinosaurs in the upper Jurassic Lourinhã formation. Portugal. *Oryctos* 8, 47–52.
- Matsukawa, M., Shibata, K., Kukihara, R., Koarai, K., Lockley, M.G., 2005. Review of Japanese dinosaur track localities: implications for ichnotaxonomy, paleogeography and stratigraphic correlation. *Ichnos* 12, 201–222.
- Mazzetta, G.V., Blanco, R.E., 2001. Speeds of dinosaurs from the Albian–Cenomanian of Patagonia and sauropod stance and gait. *Acta Paleontologica Polonica* 46, 235–246.
- Melchor, R.N., Valais, S., Genise, J.F., 2002. Bird-like fossil footprints from the late Triassic. *Nature* 417, 936.
- Milner, A.R.C., Harris, J.D., Lockley, M.G., Kirkland, J.I., Matthews, N.A., 2009. Bird-like anatomy, posture, and behavior revealed by an Early Jurassic theropod dinosaur resting trace. *PLoS ONE*. doi:10.1371/journal.pone.0004591.
- Molnar, R.E., 1991. Fossil reptiles in Australia. In: Vickers-Rich, P., Monaghan, J.M., Baird, R.F., Rich, T.H. (Eds.), *Vertebrate Palaeontology of Australasia*. Pioneer Design Studio, pp. 606–702.
- Molnar, R.E., 1996. Observations on the Australian ornithopod dinosaur, *Muttaborrasaurus*. *Memoirs of the Queensland Museum* 39 (3), 639–652.
- Moratalla, J.J., Sanz, J.L., Jimenez, S., 1988. Multivariate analysis on Lower Cretaceous dinosaur footprints: discrimination between ornithopods and theropods. *Geobios* 21, 395–408.
- Moratalla, J.J., Sanz, J.L., Jimenez, S., 1994. Dinosaur tracks from the Lower Cretaceous of Reguimiel de la Sierra: inferences on a new quadrupedal ornithopod trackway. *Ichnos* 3, 89–97.
- Moreno, K., Benton, M.J., 2005. Occurrence of sauropod dinosaur tracks in the upper Jurassic of Chile (redescription of *Iguanodonichnus frenki*). *Journal of South American Earth Sciences* 20, 253–257.
- Norman, D.B., 2004. Basal Iguanodontia. In: Weishampel, D.B., Dodson, P., Osmólska, H. (Eds.), *The Dinosauria*. University of California Press, pp. 413–437.
- Paik, I.S., Huh, M., Park, K.H., Hwang, K.G., Kim, K.S., Kim, H.J., 2006. Yeosu dinosaur track sites of Korea: the youngest dinosaur track records in Asia. *Journal of Asian Earth Sciences* 28, 457–468.
- Paul, G., 1988. *Predatory Dinosaurs of the World*. Simon and Shuster, New York, p. 464.
- Peterson, W., 1924. Dinosaur tracks in the roofs of coal mines. *Natural History* 24, 388–391.
- Pittman, J.G., 1989. Stratigraphy, lithology, depositional environment, and track type of dinosaur track-bearing beds of the gulf coastal plain. In: Gillette, D.D., Lockley, M.G. (Eds.), *Dinosaur Tracks and Traces*. Cambridge University Press, pp. 135–153.
- Rich, T.H., Rich, P.V., 1989. Polar dinosaurs and biotas of the Early Cretaceous of southeastern Australia. *National Geographic Research* 5, 15–53.
- Rich, T.H., Vickers-Rich, P., 1999. The Hypsilophodontidae from southeastern Australia. In: Tomida, Y., Rich, T.H., Vickers-Rich, P. (Eds.), *Proceedings of the second Gondwana dinosaur symposium*. Natural Science Museum of Tokyo Monographs 15, pp. 167–180.
- Rich, T.H., Vickers-Rich, P., 2003. A Century of Australian Dinosaurs. Queen Victoria Museum and Art Gallery, Launceston, p. 124.
- Salisbury, S.W., 2003. Theropod teeth from the Lower Cretaceous Winton Formation, central-western Queensland, Australia. In: Longman Symposium, CAVEPS 2003. Longman Symposium: Conference of Australasian Vertebrate Evolution, Palaeontology and Systematics. Queensland Museum, Queensland, Australia, pp. 18–19.

- Salisbury, S.W., Agnolin, F., Ezcurra, M., Pais, D., 2007. A critical reassessment of the Cretaceous non-avian dinosaur faunas of Australia and New Zealand. *Journal of Vertebrate Paleontology* 27 (supplement to number 3), 138A.
- Smith, N.D., Makovicky, P.J., Angolin, F.L., Ezcurra, M.D., Pais, D.F., Salisbury, S.W., 2008. A *Megaraptor*-like theropod (Dinosauria: Tetanurae) in Australia: support for faunal exchange across eastern and western Gondwana in the mid-Cretaceous. *Proceedings of the Royal Society B* 275, 2085–2093.
- Sternberg, C.M., 1932. Dinosaur tracks from Peace River, British Columbia, Annual Report National Museum Canada (for 1930), pp. 59–85.
- Thulborn, R.A., 1994. Ornithopod dinosaur tracks from the Lower Jurassic of Queensland. *Alcheringa* 18, 247–258.
- Thulborn, R.A., Wade, M., 1979. Dinosaur stampede in the Cretaceous of Queensland. *Lethaia* 12, 275–279.
- Thulborn, R.A., Wade, M., 1984. Dinosaur trackways in the Winton Formation (Mid-Cretaceous) of Queensland. *Memoirs Queensland Museum* 21, 413–517.
- Thulborn, R.A., Wade, M., 1989. A footprint as a history of movement. In: Gillette, D.D., Lockley, M.G. (Eds.), *Dinosaur Tracks and Traces*. Cambridge University Press, pp. 51–56.
- Thulborn, T., 1990. *Dinosaur Tracks*. Chapman Hall, London, p. 410.
- Wilson, J.A., Carrano, M.T., 1999. Titanosaurs and the origin of “wide-gauge” trackways: a biomechanical and systematic perspective on sauropod locomotion. *Paleobiology* 25, 252–267.

## Appendix 1

Track parameters of *Amblydactylus* cf. *A. gethingi*, Winton Formation, Lark Quarry, central-western Queensland, tracks numbered 1–11. Adapted from Thulborn and Wade (1984). Lark Quarry tracks number 4\* and 5\* adapted from Thulborn and Wade (1979). Lark Quarry tracks number 4\*\* and 5\*\* from photos courtesy of the Queensland Museum.

Track parameter	1	2	3	4	5	6	7	8	9	10	11	4*	5*	4**	5**
L	59.5	59.1	64.0	57.0	55.4	56.5	50.5	58.9	57.2	53.0	34	51.9	55.3	50.1	45.6
W	55.4	57.5	56.0	55.9	57.0	52.7	54.5	54.5	59.9	54.4	53.4	58.3	55.7	51.4	56.6
K	40.7	36.6	42.6	33.8	32.0	35.5	30.7	36.0	32.0	38.4	23.4	15.8	27.6	–	27.8
M	37.0	39.2	40.8	31.7	35.8	34.4	28.3	33.4	34.7	32.8	21.4	29.2	25.6	–	26.5
L2	50.4	44.5	52.9	38.8	41.2	39.5	38.6	40.8	45.4	42.0	29.5	45.3	36.3	36.6	36.8
BL2	11.9	9.5	11.0	6.6	10.0	6.1	7.1	6.4	13.1	5.5	5.1	14.4	4.5	13.0	8.4
WM2	13.0	9.6	14.6	8.1	7.9	8.8	9.4	7.7	9.3	8.3	10.8	15.0	6.6	9.6	6.6
WB2	18.0	14.7	19.5	13.9	15.6	16.0	14.8	13.4	14.0	14.8	15.1	16.2	13.8	11.4	13.2
L3	59.5	59.1	64.0	57.0	55.3	56.5	50.5	58.9	57.2	53.0	34.0	51.9	52.2	50.1	45.6
BL3	21.8	23.7	23.4	26.5	24.0	23.4	24.9	27.2	26.8	19.8	15.5	31.9	26.8	25.2	20.0
WM3	16.0	18.2	17.7	17.0	15.7	14.5	13.2	16.8	15.7	13.3	10.6	12.3	15.4	8.2	15.4
WB3	23.5	27.9	25.4	27.5	25.9	24.0	29.2	29.7	28.1	22.6	24.8	20.4	19.7	–	20.0
L4	44.0	47.0	48.4	39.6	47.7	44.5	34.4	39.9	51.6	40.8	26.7	44.4	43.8	–	28.5
BL4	7.3	9.0	10.0	9.3	12.3	11.8	5.7	8.5	17.1	10.5	5.3	15.5	15.9	–	15.4
WM4	7.7	11.9	10.6	10.5	12.4	10.7	6.7	9.7	14.7	11.4	8.1	10.8	14.3	–	12.9
WB4	13.6	15.9	15.8	15.0	15.1	18.5	10.5	16.5	18.6	19.6	15.4	14.5	19.1	–	15.8
L/W	1.07	1.03	1.14	1.02	0.97	1.07	0.93	1.08	0.95	0.97	0.64	0.89	0.94	0.97	0.81
L/K	1.46	1.61	1.50	1.69	1.73	1.59	1.64	1.64	1.75	1.38	1.45	3.28	1.89	–	1.64
L/M	1.61	1.51	1.51	1.80	1.54	1.64	1.78	1.76	1.65	1.62	1.59	1.78	2.04	–	1.72
BL2/WM2	0.92	0.99	0.75	0.81	1.27	0.69	0.76	0.83	1.41	0.66	0.47	0.96	0.68	1.35	1.27
BL3/WM3	1.36	1.30	1.32	1.56	1.53	1.61	1.89	1.62	1.71	1.49	1.46	2.59	1.74	3.70	1.30
BL4/WM4	0.95	0.76	0.94	0.89	0.99	1.10	0.85	0.88	1.16	0.92	0.65	1.44	1.11	–	1.19
L2/WB2	2.80	3.03	2.71	2.79	2.64	2.47	2.91	3.04	3.24	2.84	1.95	2.80	2.63	3.21	2.79
L3/WB3	2.53	2.12	2.52	2.07	2.14	2.35	1.73	1.98	2.04	2.35	1.37	2.54	2.65	–	2.28
L4/WB4	3.24	2.96	3.06	2.64	3.16	2.41	3.28	2.42	2.77	2.08	1.73	3.06	2.29	–	1.80